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BIOLOGY OF THE PAPAYA FRUIT FLY, *TOXOTRY-
PANA CURVICAUDA*, IN FLORIDA.

By ARTHUR C. MASON, *Assistant Entomologist, Fruit-Insect Investigations,
Bureau of Entomology.*

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INTRODUCTION.

The occurrence in 1905 of a newly introduced species of fruit fly (*Toxotrypana curvicauda* Gerst.)¹ attacking the papaya (*Carica papaya* L.) in south Florida was the occasion several years later for a preliminary investigation and paper on the insect by Knab and Yothers.² Technical descriptions of the insect, together with its distribution and history, are recorded therein, and also some notes on its habits. In recent years the pest has assumed much greater economic proportions, due to the increasing production of the papaya from a commercial standpoint, and also to the spread of the insect over nearly all portions of the State where papayas are grown. Hence a careful study of its biology and control was undertaken by the writer.

It is the purpose of this bulletin to present an accurate account of the life history and seasonal history of the insect, together with its habits and the factors influencing its development and spread. The methods of control as far as worked out are also given.

¹ Dipterous family Trypetidae.

² Knab, Frederick, and Yothers, W. W. Papaya fruit fly. In Jour. Agr. Research, vol. 2, No. 6, p. 447-454, pl. 41-42. 1914. Literature cited, p. 453.

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DESCRIPTION AND LIFE HISTORY.

EGG.

The eggs (Pl. I, C, *b*) are of very unusual proportions, being long and slender, somewhat club-shaped or fusiform, with a long cylindrical stalk. The average length is about 2.5 mm. and the greatest diameter is 0.2 mm. They are inserted into the seed cavity of the fruit from the long ovipositor of the female. The stalk sometimes remains partly in the flesh, although the eggs are never placed there as the young maggots seem unable to survive there. They always occur in clusters, and usually there is only one cluster to a fruit. The cluster consists of from 6 to 20 or more eggs, which are always fastened together by an adhesive substance on the surface of the eggs. One female, according to Knab and Yothers, is capable of laying 103 eggs, all of which are disposed of at about the same time.

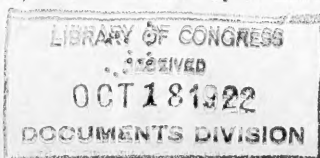
The eggs require from 12 to 14 days to hatch at any time throughout the year. Although the other stages are longer in winter than summer, the egg seems not to be affected by climatic changes. This point was determined by cutting open infested fruits at definite intervals after they were stung. Usually an adult would oviposit in several fruits on a tree the same evening. It was then possible to cut one of these on each of several successive days until the eggs were found to have hatched. Even in the fruits which had been cut the eggs would complete their development if the halves were placed together, provided they were several days old when first exposed to the light and air. With freshly laid eggs this was not found to be true. Many attempts were made to rear the eggs artificially after removing them from the fruit but without success. When dissected from the fruit and placed on a piece of leaf or fruit pulp over a plug of wet cotton in a vial inverted in water, as practiced by Back and Pemberton³ with melon-fly eggs in Hawaii, they failed to develop. Even though the conditions of heat and moisture were apparently the same as in the fruit they did not hatch.

When ready to hatch the eggs split longitudinally along the micropylar half and the maggot escapes, leaving the stalk end intact.

LARVA.

The young maggots on hatching from the eggs begin at once to feed on the coating of the seeds. They remain for about the first half of their existence within the seed cavity, feeding on the seed coverings and other fibers there. Many of the seeds become de-

³ Back, E. A., and Pemberton, C. E. The melon fly in Hawaii. U. S. Dept. Agr. Bul. 491, p. 18. 1917.



tached by this process, and the loose seeds in the fruits serve as an indication of their presence. When newly born the maggots are almost transparent, but soon assume a shining, dirty white color while in the seed cavity. Later on, as they continue to develop, they eat into the flesh of the fruit, first close to the cavity and then working farther out until, when mature, they are close to the skin. They have then only to eat a hole through the rind to escape. During this latter part of their life they become a rich golden yellow color, like the color of the fruit on which they are feeding. The presence of the maggots in the fruit usually causes it to turn yellow and ripen prematurely. This is a distinct advantage to the larvæ, for they do not like the juice of the green fruits and usually remain around the seed cavity until the flesh begins to soften.

The mature maggots (Pl. I, C, *a*) average about 11 mm. in length, are subcylindrical in shape, and taper anteriorly to the mouth.

The length of time required for their development varied from 10 to 27 days in a large number of tests. The cooler weather of winter prolongs somewhat the length of the larval stage. Conditions unfavorable to the larvæ, such as the fruit decaying or the maggots being removed from the fruit, will cause them to transform before the normal time. On the other hand, if the conditions are favorable the larvæ may remain in the fruit for several days after reaching maturity. The average time for this stage is 15 days.

They make their escape by eating a hole through the skin and dropping to the ground. As a rule, when one escapes the others will follow in rapid succession, and often all emerge from the same exit hole. If the fruit has already fallen from the tree the maggots go into the ground immediately under it; if the fruit is still on the tree they drop to the ground. Often a larva will remain partly emerged from a fruit and continue a wriggling, twisting motion for an hour or more before finally dropping. When once on the ground the maggots immediately bury themselves and never wander around on the soil. The transformation is completed within a few hours after entering the ground. The period of exposure from the time of leaving the fruit to entering the soil ordinarily would be only a minute or two, and consequently there would be little chance for parasitism here. Very rarely a maggot will pupate inside a fruit.

The number of maggots in a single infested fruit sometimes runs up as high as 40, although ordinarily there are about 15 or 20. A very small fruit may have only 2 or 3.

If confined in breeding jars where no soil is present the larvæ usually will not pupate. In a glass stender dish or Petri dish the mature maggots would remain in the larval stage for three or four days, continually crawling around the dish. After several days they

attempt to pupate, but many of them die before completing the transformation. Even when they succeeded in pupating, the adults never matured from them. Evidently this is due to a lack of moisture, which seems to be a vital factor to all stages of development in this insect.

PUPARIUM.

In common with other fruit flies, this insect passes the pupal stage in the ground. The puparia occur naturally under the infested trees in the soil, for, as stated above, the maggots do not travel around, but go into the ground where they fall. The average depth of the puparia is 2 inches, although they vary anywhere from the surface to 3 inches deep, and sometimes occur also under rock and rubbish on the surface. The moisture in the earth seems to determine largely this point, for they go down until they can get into damp soil. Very rarely one is found inside the fruit either on the tree or on the ground.

The puparia (Pl. I, B) are of a stout, subcylindrical form with rounded ends and vary in length from 8.5 to 12 mm. The size is no indication of sex, for from 100 of the smallest ones obtainable about an equal number of males and females emerged. The color of the puparia varies all the way from a light ferruginous yellow to dark brown or almost black. This color in no way indicates their age, for some remain light colored throughout their existence.

The pupal stage was found to vary from 18 to 44 days in breeding out several hundred in all months of the year. Aside from the temperature changes the effect of the moisture is a very large factor in this regard. Under favorable conditions of moisture the largest number of the adults will emerge after 18 to 20 days in hot weather, but in winter this runs up between 30 and 40 days on the average. Hooker⁴ found it to last from 17 to 21 days in Porto Rico. Moisture, even more than heat, seems to be the determining factor. Lack of moisture will prolong very materially the pupal stage and if continued will prove fatal. On the other hand, excessive moisture will kill the puparia. The following data prove this point:

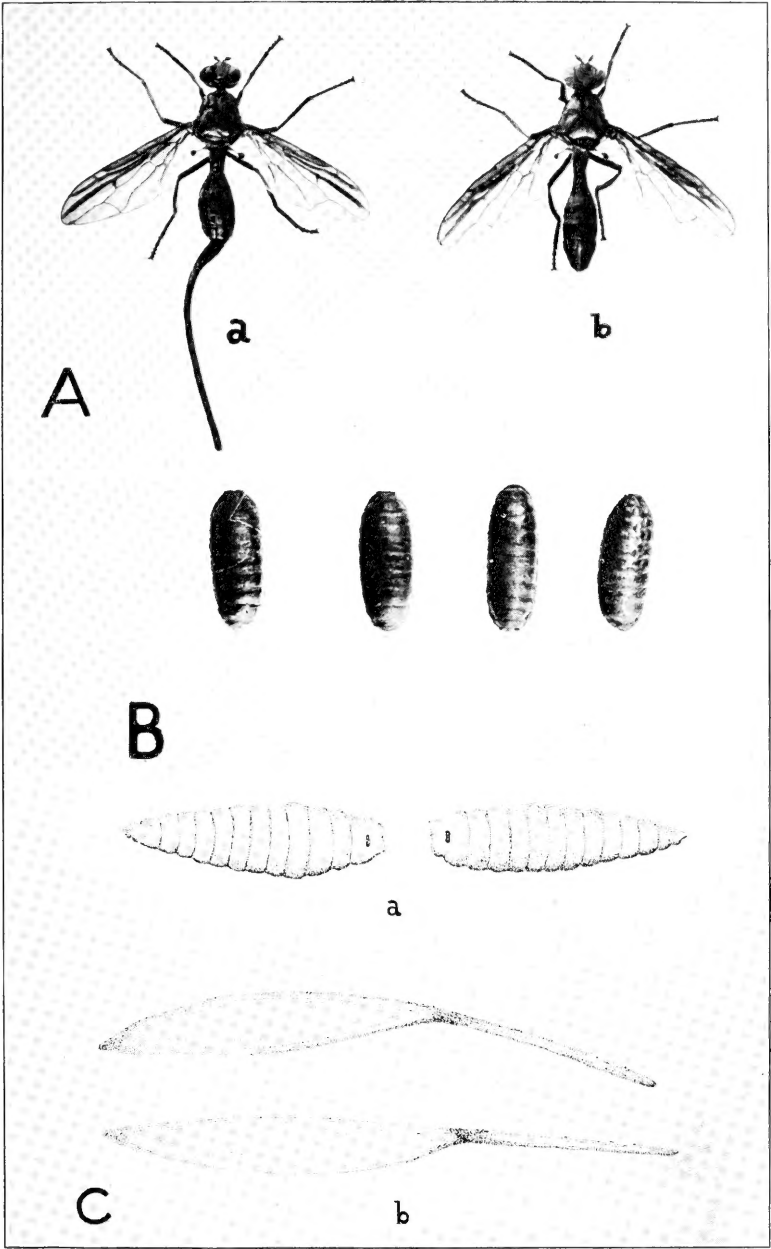
One hundred fresh puparia placed in soil in a jar and kept without any water being added. All died.

One hundred fresh puparia placed in soil in a jar and kept moderately moist; 80 adults emerged, 20 died.

One hundred fresh puparia placed in soil in a jar and kept wet every day. All died.

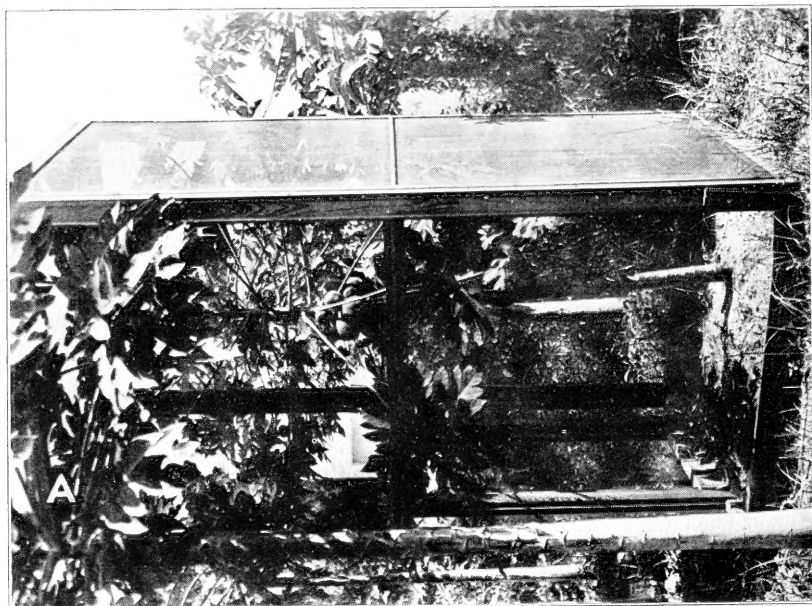
Even under the most favorable conditions of heat and moisture the puparia do not all mature, and 70 per cent is a very good average. Under natural conditions the average runs below that. Sev-

⁴Hooker, C. W. Fruit flies. In Porto Rico Agr. Exp. Sta. Ann. Rpt. 1912, p. 36. 1913.



TOXOTRYPANA CURVICAUDA.

A, Adult flies: a, Female; b, male. $\times 2$. B, Puparia. $\times 1\frac{1}{2}$. C, a, Larvae, $\times 2$; b, eggs, $\times 20$



TOXOTRYPANA CURVICAUDA.

At left, type of cage used for rearing papaya fruit flies in fruits on the tree. At right, papaya fruits after being stung, showing characteristic exudate of milky fluid caused by the females puncturing the skin. (Photo by G. F. Moynette.)

eral hundred puparia placed in jars, some of them reared from larvæ and others gathered in the soil under trees, gave results as shown in Table I.

TABLE I.—*Males and females of Toxotrypana curvicauda maturing from puparia placed in jars.*

Number of pupæ.	Number of males.	Number of females.	Total emerged.	Total died.
870	279	281	560	310

Thus it is seen that only 64.3 per cent matured into adults, while 35.7 per cent died. Of the number maturing practically 50 per cent were males and 50 per cent females.

Practically all the adults emerge from the soil in early morning just before daylight. Very rarely will one emerge between sunrise and midnight. The adults often carry the pupal case to the surface of the ground before freeing themselves from it. Only a few minutes are then required for their complete development.

ADULTS

The adult of this species (Pl. I, A) is a wasplike fly, very much resembling in coloration and general appearance the wasps of the genus *Polistes*. The body is yellow and brown, marked with black, and the females are made strikingly conspicuous by a long, curved ovipositor, even longer than the body itself. There is considerable variation in the size of the flies, but they average about 12 mm. in length. The ovipositor of the female varies from 10 to 14 mm. in length.

The flies exhibit a rather rapid flight and walk with a quick nervous motion. The females are not often seen on bright days but appear about the trees to lay their eggs in the late afternoon or evening. They show a negative reaction to sunlight and always seek the shady side of the tree or fruit. Although sometimes seen during the morning and noon hours, the greatest flight occurs about an hour before sunset. The males, however, are more active on bright days. Both sexes are easily disturbed when resting on the fruits.

The life of the adult flies is probably only a few days in length. They have been kept alive in captivity for 31 days when properly fed, although the average is very much less. The flies will eat any kind of sugar sirup and the pulp and juices of some fruits, but they never appear to be attracted by any food. Many will die without

* For original description see Gerstaecker, A. Beschreibung einiger ausgezeichneten neuen Dipteren aus der familie Muscariae. In Ent. Zeitung Stettin, Jahrg. 21, No. 4/6, p. 194-195. 1860.

ever eating when food is placed at their disposal. Others will eat only when food is placed directly in front of them or when they happen to walk into it. When they have once tasted the sweets they will feed until the body is well distended. The best results were obtained by placing drops of brown-sugar sirup on the net or screen covering of the cages. In the large cages it was sprayed with an atomizer on the under side of the leaves of the tree. The flies have a liking for the pulp of ripe papayas and also eat bananas but will not eat the juice of oranges.

The following figures show the length of life of some of the flies:

Fifty-four flies confined without food after emerging lived from 1.5 to 5.5 days, with an average of 3.45 days.

Thirty-six flies given water only lived from 3 to 6 days with an average of 4.6 days.

Seventy-six flies fed on sugar sirup lived from 3 to 31 days with an average of 7.4 days.

Under natural conditions these figures probably do not vary much. Five to seven days represent an average life for the adult.

COPULATION.

The insects copulate usually on the leaves or fruits of the papayas, but can only rarely be observed. Copulation takes place during the daytime, for the male is more active then, as noted above. He seems to experience some difficulty in holding the female in position because of the long ovipositor. To accomplish his object, he alights on top of the female and, clasping her body with the first two pairs of legs, he draws the ovipositor back and up with the remaining pair. Then by practically standing on his head he is able to bring the tip of his abdomen in conjunction with the end of the ovipositor. They usually hold this position for several minutes or longer, one pair being observed to remain for nearly two hours. If disturbed the female will walk around the fruit or even fly to another tree, always carrying the male along in position. In captivity the flies very seldom copulate. This is true when confined in the large cages over the trees (Pl. II, at left) as well as in small cages or jars in the laboratory. Of several hundred adults bred out in jars and observed at all hours of day and night, only a very few ever made any attempts at copulation. These cases happened when the flies were 4 or 5 days old and had been fed on sugar sirup or fruit pulp. If given no food they soon die without mating.

OVIPOSITION.

Oviposition usually takes place in the evening, that being the time the adult females are most active. It has been observed occasionally, however, to take place at all other times of the day. The fruits selected by the females in which to lay their eggs are

usually medium or larger sized, if all sizes are present on the plant. They often begin work on a plant when the fruits have just set and are very small, and all sizes of fruits are subject to attack. They seem, however, to prefer the half-grown or larger fruits, perhaps due to a natural instinct, for if the eggs are deposited in a nearly mature fruit, the fruit may ripen and decay before the maggots have completed their growth. On the other hand, if placed in very small fruits the maggots will mature before the fruit has started to ripen, and they sometimes experience difficulty in escaping from green fruits. It has been said that the milky juice from the green fruits is fatal to the larvæ, but this has not been found to be true. In fact, maggots which had been rolled around in the juice from green fruits completed their development.

It is not often that an adult fly will oviposit in a fruit where eggs or maggots are already present, although in a few instances maggots of two distinct sizes were found. When the first ones to mature escape they cause the fruit to decay, so the younger ones may not be able to complete their development.

The adult fly alights on the fruit selected and usually walks around for a time with a nervous motion. When she has found a suitable place she forces her ovipositor through the skin and flesh of the fruit and deposits her eggs inside in the seed cavity. This is accomplished by raising the long ovipositor up in a curved position and placing the tip of it on the fruit near the end of the abdomen, then forcing it through the fruit. The position taken is much the same as that of the ichneumon flies in depositing their eggs.

The eggs are laid in clusters and ordinarily only one cluster will be placed in a single fruit, although occasionally two or three are found. The fly often stings a fruit several times, as many as 10 punctures being counted at times, but does not always deposit a cluster of eggs. Possibly she is not able to reach through the flesh of the fruit in all places and hence withdraws and seeks a new place. In fact, many fruits are stung several times and no eggs laid in them. This has often happened in the breeding cages where fruits supposedly containing eggs failed to develop any maggots. Also many fruits on the trees have been marked after being stung and no larvæ ever appeared in them. Usually about two minutes are required by the female to deposit the eggs, although instances have been noted where the ovipositor remained inserted for an hour or more. Occasionally a female will become trapped and die in the milky juice which wells up when the skin is punctured. This exudate coagulates and holds the fly if she does not soon escape. Whenever a fruit is stung the exudate produces a characteristic mark by running down the side of the fruit and also coagulating in a large

drop at the puncture. (Pl. II, at right.) It is possible thereby to determine easily the number and location of the punctures.

SEASONAL HISTORY AND OCCURRENCE.

The insects breed throughout the year in Florida and are present in all stages at any month of the year. They have, however, some seasonal preferences and occur in much larger numbers at some seasons than others. The time of greatest flight of the adults seems to be during March and April, while in late summer and fall there are very few of them in evidence. This is correlated largely with the growth of the host plants, which begin fruiting usually in the fall and continue through the winter and spring. Many of the plants die down or are cut out in the late spring and new ones set. The flies therefore appear on the new fruits in the fall and continue to breed in increasing numbers throughout the winter and spring. The wild papayas in the hammocks fruit at all seasons and always serve as hosts whether or not any of the cultivated sorts are available. The generations are by no means marked and vary in length from 40 days in summer to 70 or more in colder weather. In a year's time there are about six generations, although they overlap and are in no way distinct. Moisture in the soil is a very important regulating factor in the length of all stages, perhaps even more so than changes of temperature.

POWER OF FLIGHT.

The distance which the adults are able to travel is not very great, for they are not strong fliers. One planting of papayas under observation was placed 2 miles from where any other plants existed and remained free from infestation throughout the season, the adults apparently being unable to cover that distance. In most locations, however, there are wild papayas all through the surrounding hammocks, and these serve to harbor and spread them.

SUSCEPTIBILITY OF VARIETIES.

While no distinct varieties of the papaya (*Carica papaya*) are recognized, there are several types of the fruit grown in the State. Several have been introduced from foreign countries and crossed on existing types. Then there are the original wild plants which have been cross-pollinated on the cultivated plants through natural agencies. Through all this cross-pollination there result two rather distinct types of fruits, one the small, round, or oval type with rather thin skin and flesh and the other the large, oblong fruits which usually have thick flesh. One especially fine fruit of the latter type has been produced at the Plant Introduction Gardens at Miami, Fla.,

by Mr. Edward Simmonds, and is known as No. 28533. These oblong fruits are much more immune to the attacks of the flies, due largely to the fact that the female flies are unable to reach through the flesh of the fruit with their ovipositors and lay their eggs. In fact, in some places they were found practically free from infestation and are considered immune by the growers. An examination of about 300 fruits of all kinds on the Florida Keys, by A. L. Swanson, an inspector of the State Plant Board of Florida, showed 90 per cent of infestation in the small round fruits as compared to no infestation in the large oblong fruits. This latter fact has not held good, however, in investigations by the writer. Several hundred fruits examined both on the keys and in many places on the mainland showed about 88 per cent of the round or oval fruits infested and about 15 per cent of the oblong fruits infested. In wild fruits in the hammocks the infestation is close to 100 per cent. No papayas grown in the State are entirely immune from the attack of the flies.

ENEMIES.

Only two natural enemies have been noted on this insect, one the jumping spiders and the other the small red ants which sometimes prey upon the larvæ. The large black jumping spiders conceal themselves between the fruits on the tree and are then able to catch the flies when they alight near them. Doubtless they destroy many in this way. On a few occasions ants have been observed attacking the maggots in a fruit which had fallen to the ground. They enter through the exit hole of the first maggot to escape and can then destroy the remaining larvæ in the fruit. They represent a negligible factor, however, in the control of the pest.

Six hundred pupæ dug from the soil under the trees and bred out in jars failed to produce a single parasite. The insect is well protected from the attack of parasites through nearly the entire period of its life.

CONTROL MEASURES.

The most effective way of preventing injury from this pest is by bagging the trees or fruits. Either cheesecloth or mosquito netting can be tied over the trees or around the individual fruits, and the flies will not try to sting the fruits through it. However, this plan is hardly practicable on a large scale, since it requires considerable work and expense and, in many cases, changing the bags as the fruits grow larger.

The adults are readily killed by feeding them a poisoned sirup, the best results being obtained by using sodium arsenite or potassium arsenate dissolved in brown sugar sirup. When given this sirup the adult flies die very soon after feeding, and they eat it as readily

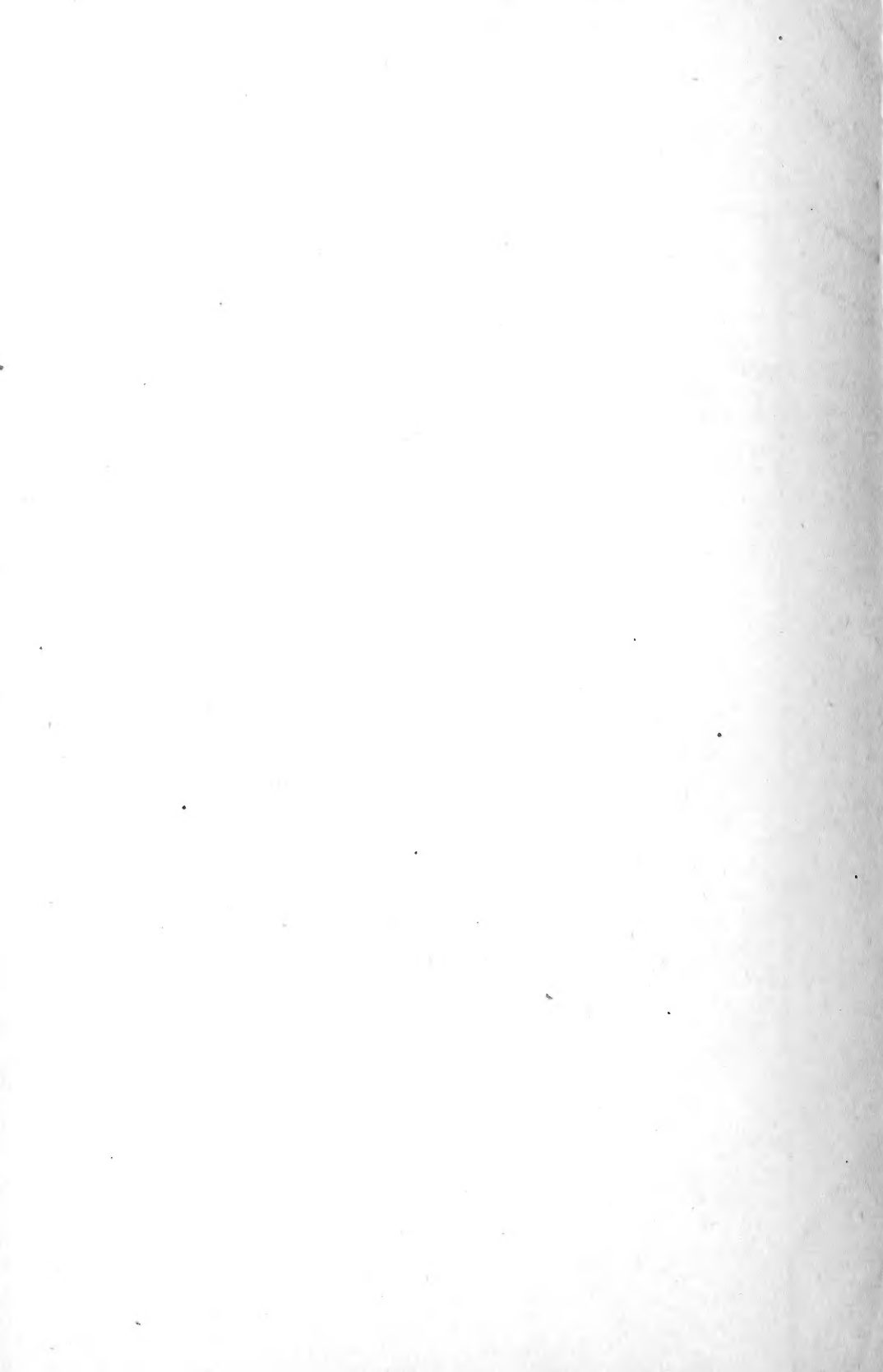
as the plain sirup. Very good killing results were also obtained by spraying this mixture with an atomizer on the under sides of the leaves of the trees in the large cages. Large numbers of flies were found dead on the ground within a couple of hours. These soluble poisons, however, burn the trees very severely and can not safely be used. Even at the rate of 1 pound to 50 gallons, which is as weak as can be effectively used, severe injury was noted. Insoluble arsenic compounds such as Paris green, arsenate of lead, arsenate of calcium, and arsenite of zinc do not damage the trees but are not effective. When the arsenic is mixed in the sirup the flies do not get enough to kill them.

The following plan if carried out thoroughly will very materially reduce the number of flies and make the growing of papayas practical and profitable: (1) Selection of good seed and production of fruits of oblong shape and thick flesh which will offer more or less immunity to attack; (2) conscientious destruction of the infested fruits on the trees early in the season and before the maggots escape into the ground; (3) destruction of all inferior plants and wild plants around the place which might serve to breed the pests.

If a planting is sufficiently isolated from other papayas the flies may be killed out by destroying all the plants in the spring, about April or May, and resetting new plants. These young plants will begin to fruit in the summer or early fall, but there will be a period of about 60 days when no fruits are present, which is long enough to starve out the flies. Along with this program should go the destruction of all wild plants in the hammocks for a radius of at least 2 miles. One large planting under observation was kept free from infestation for the entire winter by this method and a good crop of fruit obtained. The previous winter and spring the plants were badly infested, but the pests were entirely starved out during the summer. In most locations, however, a grower would not be sufficiently isolated to practice this method successfully unless the cooperation of his neighbors could be enlisted.

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